

FOREST VEGETATION OF THE COLORADO FRONT RANGE: PATTERNS OF SPECIES DIVERSITY*

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Introduction

Wealth in species is a measurable attribute of a plant community resulting from the combined effects of such processes as immigration, resource partitioning, competition, adaptation, speciation and extinction. The assumed potential of species diversity measures to aid in understanding these processes has prompted extensive research to document changes in plant diversity across compositional and environmental gradients. However, despite the considerable effort expended, a unified theory of plant species diversity has not yet emerged. While work with other groups of organisms, notably birds, has led to increased understanding of community structure (e.g. Cody 1975, Karr & Roth 1971, MacArthur 1961, Recher 1969, Whittaker 1977), results from plant diversity studies have only suggested a wealth of variation, often interpretable at the local level, but without consistent pattern (Glenn-Lewin 1977, Whittaker 1977).

During investigations of forest vegetation of the northern Colorado Front Range, variation in plant species diversity was observed to be correlated with successional development, elevation, and site moisture conditions. However, many of the patterns observed appeared at variance with those usually reported or postulated in the literature. An examination in depth was undertaken to 1) document these patterns, 2) relate them to previously proposed theories of plant species diversity and 3) consider their implications for future studies of plant species diversity.

Methods

Vegetation analysis:

Inconsistent results of published studies of variation in species diversity along environmental gradients suggested the need to examine such variation in a multidimensional framework. Gradient analysis methods were selected as ideal for this purpose (Whittaker 1967, 1973).

The analysis is based on 305 samples of 0.1 ha collected as part of an intensive study of forest vegetation of the northern Colorado Front Range (Peet 1975). The sampling units were 20 × 50 m rectangles with 25 contiguous 0.5 × 2 m subplots located along the center line. Understorey importance (leaf area below 1 m) was measured as percent cover within the 25 subplots. Additional species occurring in the plot were recorded as present but no cover values were assigned. Cover above 1 m was estimated along a 50 m line transect. All trees present in the plot were recorded by species and diameter. Sample placement was stratified by elevation, moisture-exposure and stand age to assure coverage of a maximum range of forest variation. (Details of the sampling methodology are available in Peet 1975 and will be published elsewhere.)

Because preliminary studies showed elevation and moisture to be the site variables most closely related to forest variation, these factors were selected as axes for a two-dimensional gradient model. Whereas elevation was easily measured for each site, no simple measure was available which incorporated all the important components of site moisture. As an alternative to direct measurement, ordination was used so as to allow vegetational variation to define the gradient. The vegetation samples were separated into seven 200-m elevational strata so as to remove most of the variation attributable to elevation. Within each stratum

* Nomenclature follows Weber (1976).

the stands were ordered by correspondence analysis (=reciprocal averaging, Guinocet 1972, Hill 1973a, 1974) using understory (< 1 m tall) data. Work by several authors (Fasham 1977, Gauch et al. 1977, Hill 1974) has shown this method, when applied to unidimensional gradients, to be largely free of the distortions arising from the nonlinearities of vegetational data which diminish the effectiveness of most other ordination procedures. Comparison with a scalar derived from potential incident solar radiation (as calculated from slope and aspect) and subjective indices of slope position and exposure showed the resultant stand sequences to be significantly correlated (Spearman rank correlation, $P < 0.05$) with site moisture. However, because correspondence analysis is valuable only as an ordering method, it was necessary to scale the resultant ordination sequences against a standard gradient using curve-fitting methods. The previously mentioned site moisture scalar was used as the standard for this purpose. The rescaled stratal gradients were then combined to form a two-dimensional gradient representation of forest vegetation. This representation forms the background for figures 1, 2 and 4 (more details are available in Peet 1975).

Successional trends in Front Range forests are not easily quantified because of the stochastic nature of the successional process and because of the compounded effects of time, elevation and moisture. Moreover, as forest composition and structure depend heavily on initial conditions of forest establishment, unique successional patterns cannot be specified. The approach used in the present study was to age selected canopy trees and to examine tree diameter distributions for large numbers of stands. Together, these were used to construct hypothetical developmental sequences of stands for particular site conditions. While not unique for the sites considered, these sequences were constructed to represent the average or most frequently encountered successional patterns.

Biomass and production of forest trees are also difficult to measure. Whittaker & Marks (1975) have, however, suggested estimates based on parabolic volume (one half the basal area times the height of the tree) and estimated volume increment (one half the annual basal area increment times the height of the tree) to be reasonable approximations for comparative studies. For 27 stands representing a range of forest types, parabolic volume and estimated volume increment were determined based on samples of approximately 100 randomly selected trees per site.

Diversity Measurement:

Community diversity (alpha diversity of Whittaker 1960, 1972) was measured both as richness-diversity and as heterogeneity-diversity (sensu Peet 1974). Richness was measured as the number of vascular plant species per 0.1 ha sample unit. (Species richness in 1 and 25 m² sample units was also examined for each of the study sites but the patterns observed did not differ significantly from those obtained using 0.1 ha units.) Heterogeneity-diversity, which combines both species richness and evenness, was calculated using Hill's (1973b) first and second order diversity numbers [$N_1 = \text{Exp}(H')$ where $H' = -\sum p_i \ln p_i$; $N_2 = 1/\lambda$ where $\lambda = \sum p_i^2$; p_i being the proportional importance of the i^{th} species]. Species importances were based on percentage cover.

Isopleths of equal richness and of heterogeneity-diversity were plotted on the gradient representation as a means of examining the relationships between diversity and gradients of moisture and elevation. For this purpose a computer surface mapping routine (STAMPEDE) was employed. The resultant surface plots were partially smoothed by hand to compensate for the inability of the routine to smooth near plot edges.

Whittaker defined beta diversity as diversity across an environmental or compositional gradient. This 'gradient diversity' has often been measured as the rate of compositional change (Bratton 1975, Cody 1975, Whittaker 1960, 1972) or alternatively as gradient length (Whittaker 1972, del Moral 1972, Gauch & Whittaker 1972). Use of rate of change implies knowledge of appropriate scaling for the gradients being studied. As 'gradient scaling must be arbitrary, gradient length is a more satisfactory and readily interpretable measure. Typically gradient length is measured in half-change units where half-change refers to that distance along a gradient at which some measure of similarity (such as percentage similarity) indicates composition has changed by 50%.

Because beta diversity is a measure of change along a single gradient, care must be taken to avoid variation in other environmental factors. For this reason the data were stratified to separate the effects of moisture and elevation. The moisture and elevation gradients were broken into five and six equal segments respectively, with the lower elevation limit placed at 2300 m (insufficient data were available for forests between 1700 and 2300 m). For each pair of adjacent gradient segments percentage similarity was calculated for the average composition of the stands occurring within the segment using importance values

standardized by species totals. The resultant similarity values were subtracted from 100 to provide a measure of distance and subsequently converted to half-changes, a more linear unit of compositional change (1 half-change = dissimilarity of 50%). The smallest dissimilarity encountered (0.43 hc) was subtracted from each of the comparisons to correct for differences attributable to sampling error alone. A similar correction for 'internal dissimilarity' is used with similarity values applied to ordination problems (see Gauch 1973). The half-change distances between segments were summed to determine the length of each of the six elevational and five moisture gradients.

Results and discussion

Gradient Patterns:

Diversity has been observed to vary across moisture gradients, and several workers have reported maximum diversity in the most mesophytic* communities of a region (Brünig 1973, Carbiener 1970, Glenn-Lewin 1975, van der Maarel 1971, Ogawa et al. 1961, 1965, Risser & Rice 1971, Terborgh 1973) including workers in coniferous forests similar in structure to those of the Front Range (Daubenmire & Daubenmire 1968, Ilvessalo 1922). However, other workers have reported diversity to peak in the intermediate region of a mesic to xeric moisture gradient (Auclair & Golf 1971, Curtis 1959, Daubenmire 1970, Monk 1965, 1967, Whittaker 1956, Whittaker & Niering 1965, Wikum & Wali 1974). The latter situation has been suggested to be a response to the thinner forest canopy encountered on dry sites which allows increased light penetration and consequently greater understory development (Auclair & Golf 1971, del Moral 1972). Lowest diversity has usually been found on xeric sites but in some coniferous forests lowest diversity has been reported from intermediate situations (del Moral 1972, Daubenmire & Daubenmire 1968).

Examination of variation in species richness of Front Range forests relative to the moisture gradient (Fig. 1) suggests no single pattern. Rather, the diversity-moisture relation changes with elevation. In high elevation forests immediately below the krummholz or alpine-transition

* Mesophytic is used here to imply the middle and most favorable portion of a moisture gradient in a universal sense, with the consequence that the mesophytic sites of the generally xeric Front Range forests are located near the moist end of the gradient.

zone the richest forests are on wet, boggy sites and richness progressively decreases toward the xeric end of the gradient. At middle elevations lowest richness is generally found near the central portion of the moisture gradient and the highest diversity sites occur near the moist end. (Note that sites too wet to support forest vegetation were not included in the analysis.) The gradient position of those sites with lowest diversity values shifts progressively toward the mesic end of the gradient with decreasing elevation. These observations suggest that generalizations about diversity-moisture relationships reported for other vegetation types do not apply to the Front Range forests, and that any generalizations made outside of a multi-dimensional, environmental context will be ambiguous and over-simplified. No one relationship satisfactorily describes the variation in diversity along a moisture gradient; interaction with elevation must be considered.

Similar difficulties exist with regard to diversity patterns along elevational gradients (Fig. 1). Reed (1969), Whittaker (1956, 1960) and Yoda (1967) have reported species diversity to decrease with increasing elevation. However, in dryer areas, diversity frequently peaks at the intermediate elevations (Daubenmire 1970, Daubenmire & Daubenmire 1968, Whittaker & Niering 1965, 1975). The latter pattern has been suggested to result from herb species richness reaching a local maximum where the tree stratum is reduced and the canopy is open (Daubenmire & Daubenmire 1968, del Moral 1972, Whittaker & Niering 1965).

In Front Range forests, the relationship between richness and elevation varies with location on the topographic-moisture gradient. On xeric sites diversity decreases steadily with increasing elevation. Near the center of the moisture gradient diversity is low at middle elevations but high in both the upper and lower forest transition zones. On wet and mesic sites diversity appears to peak in the lower middle-elevations and decrease with both increasing and decreasing elevation. Independent studies of the alpine zone of the Front Range (Kiener 1940, Willard 1963) suggest a decrease in richness with further elevational increase in all moisture classes. Again it appears that generalizations made outside a regional, multidimensional context of vegetation response to environmental gradients are simplistic.

At a more general level of abstraction Terborgh (1973) has postulated on evolutionary and biogeographical grounds that the most widespread or environmentally intermediate communities within a region should be the most diverse. Examining the generalized species rich-

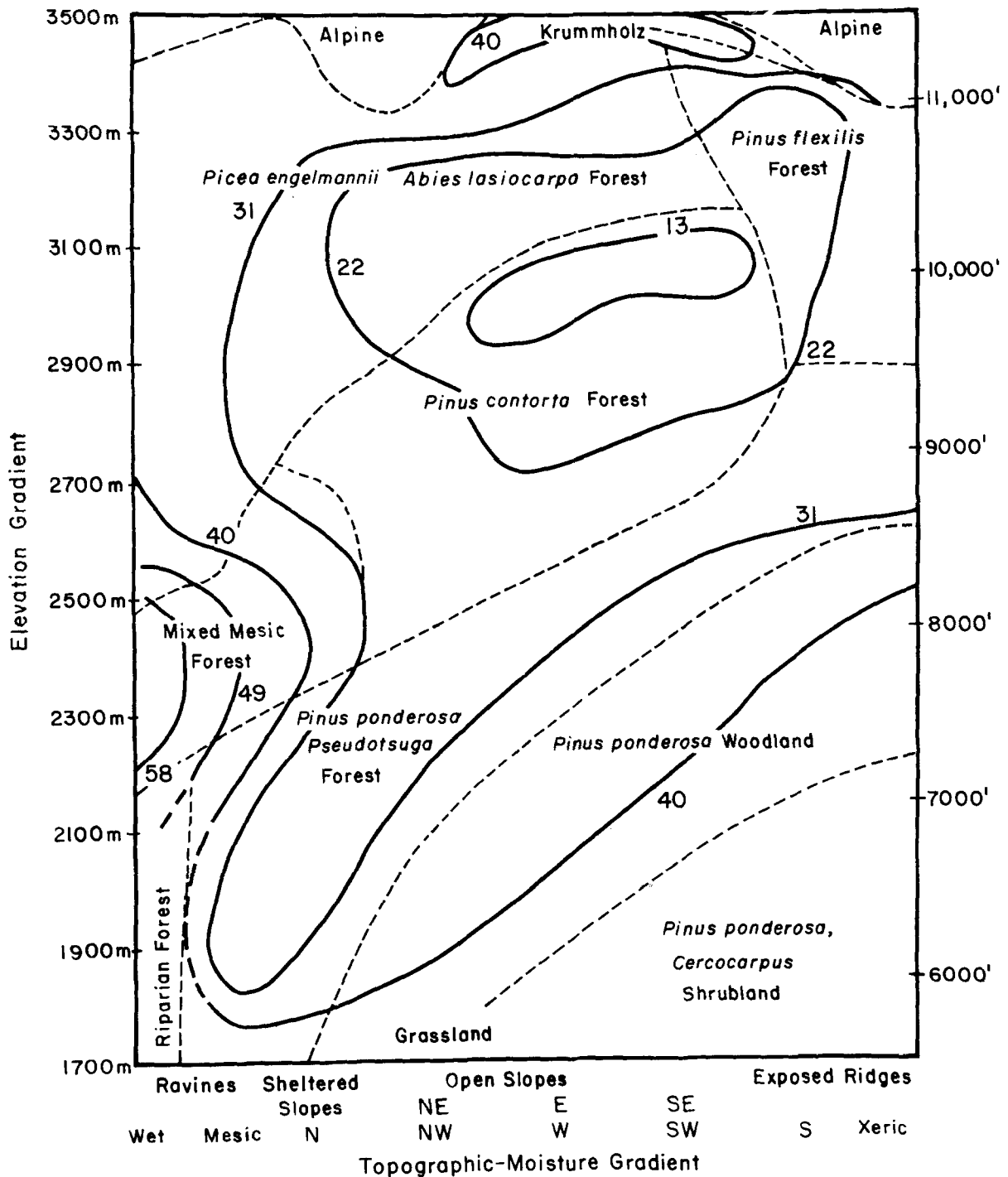


Fig. 1. Variation in species richness relative to elevation and topographic moisture gradients. Solid lines are species richness isopleths starting at 13 species per 0.1 ha and increasing by increments of 9 species. Dashed lines denote boundaries of forest types as identified in the figure. No one relationship suffices to describe changes in species richness along the moisture gradient or the elevation gradient. The two dimensional representation shows richness to be lowest in the central portion of the mosaic, with high values in peripheral sites.

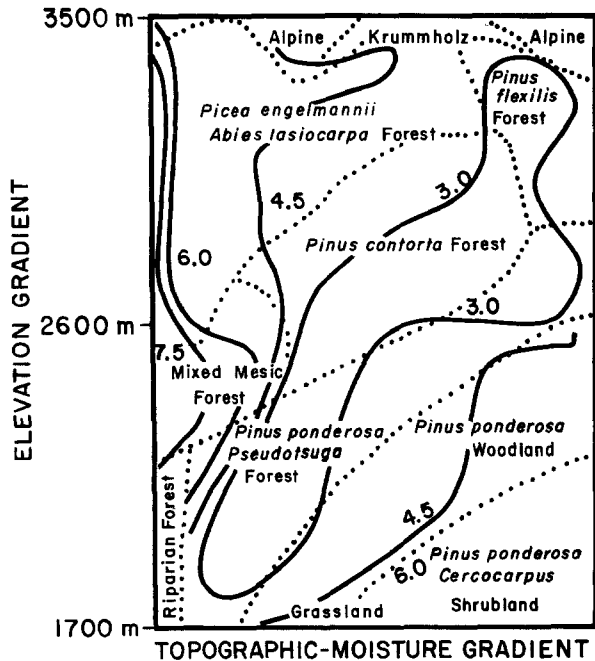


Fig. 2. Heterogeneity-diversity ($1/\sum p_i^2$, the reciprocal of Simpson's index) relative to elevation and moisture gradients. Values are lowest in the central portion of the mosaic and highest for peripheral sites.

ness patterns in Fig. 1 we find the overall pattern is one of a basin-shaped surface sloping away from a high point on the rim in the lower to mid-elevation wet-mesic forests. Thus, in contrast to Terborgh's predictions, the most central (and most wide-spread) community types appear to have the lowest richness while the peripheral types have markedly higher richness.

Variation in heterogeneity-diversity (Hill's N_2 ; reciprocal of Simpson's index), a measure incorporating both the evenness of species cover values and the absolute number of species in a community (Peet 1974), is shown in Figure 2. Examination of this plot shows the lowest diversity again located in the central region of the gradient representation, but at lower elevation than was the case for species richness. The lowest values for species richness correspond to *Pinus contorta* forests successional to *Abies lasiocarpa* and *Picea engelmannii* often with a well developed understory of *Vaccinium* species. While the absolute number of species in these forests is very low, cover is often evenly distributed over up to four species. As a consequence of its sensitivity to evenness, the lowest values of heterogeneity-diversity are found in similar, centrally located forest types, but those with only one or

two tree species dominating and with *Vaccinium* being unimportant. Specifically, these are forests of *Pinus contorta*, *Pinus flexilis* and *Pseudotsuga menziesii* which change little in canopy dominance during succession. Otherwise, the patterns are very similar to those observed for species richness. As expected (Hill 1973b, Peet 1974), N_1 (exponentiated Shannon index) is intermediate between N_2 and species richness (N_0).

Generalization can perhaps be approached by reference to stress gradients. Moderate increases in environmental stress often lead to increased diversity as suggested by Auclair & Goff (1971) and del Moral (1972). While diversity can be found to vary directly with site fertility (Dahl 1957, Frydman & Whittaker 1968, Monk 1965, 1967, Prusinkiewicz 1970, Richards 1952), serpentine soils often support more diverse vegetation than adjacent sites with more favorable edaphic conditions and higher productivity (McNaughton 1968, Whittaker 1960). These studies as well as the present one suggest that where diversity is at a maximum under less than optimal site conditions, the situation typically corresponds to reduced competitive dominance by the tallest stratum, usually the trees.

Successional patterns:

Diversity has been postulated (Harger & Tustin 1973, Odum 1969) and observed (Brünig 1973, Nicholson & Monk 1974, Tagawa 1964) to increase steadily during succession toward an asymptotic climax level. A more commonly reported pattern is for diversity to increase toward a peak in the latter stages of succession and then decline with the onset of steady-state or climax conditions as seral species are lost (Auclair & Goff 1971, Bazzaz 1975, Horn 1974, Johnson et al. 1976, Loucks 1970, Margalef 1963, 1968, Shafi & Yarranton 1973, Whittaker 1972). In contrast Habeck (1968) has reported a steady decrease in diversity after initial post-fire establishment for cedar-hemlock forests of the northern Rocky Mountains.

As a means of examining changes in the diversity of Front Range forests during succession, developmental sequences of stands were constructed for various site conditions as described in the methods section. Tables 1-3 illustrate three of these sequences.

Table 1 shows a typical developmental sequence for *Pinus contorta* stands in the central portion of the gradient representation. For this sequence diversity can be seen to drop drastically from the initial post-disturbance level following canopy closure (see Taylor 1973). This drop is followed by a gradual recovery as the stand approaches

Table 1. A developmental sequence of *Pinus contorta* stands illustrating changes in forest structure and species richness.

Age (years)	Seedlings ¹ (N/ha)	Saplings ¹ (N/ha)	Trees ¹ (N/ha)	Basal Area (m ² /ha)	Species (S/0.1 ha)
42	760	2300	3260	23.1	29
90	100	530	1650	28.3	8
140	50	60	900	28.5	12
225	0	10	490	23.3	17
≈300	1470	410	540	15.1	27

¹Seedlings includes stems over 10 cm tall and under 2.5 cm diameter at 1.4 m (dbh). Saplings include stems between 2.5 and 6 cm dbh and trees include all stems over 6 cm dbh.

the climax or steady-state condition. Apparently rapid canopy closure and tree establishment during the earliest phase of forest development result in severe competitive inhibition of understory growth. This accounts both for the low diversity and the virtual absence of seedlings in many middle-age stands. Biomass (as measured either by basal area or parabolic volume) shows a rapid post-disturbance increase followed by stagnation and an eventual drop owing first to the severe competition and then to lack of regeneration. With natural thinning, the forest canopy eventually opens and understory conditions improve for tree regeneration. This change is paralleled by increases in both species diversity and tree productivity ('Estimated volume increment').

The *Pinus contorta* sequence illustrated in Table 1 shows an initial high value of 29 species/0.1 ha dropping to 8 after canopy closure and slowly increasing to 27 with the maturation and consequent thinning of the stand. Few very young stands were available for study but one site was found to have species richness values of 21, 34 and 39 sp/0.1 ha 1, 2, and 4 years respectively after a severe fire removed all living plants from the area, thus suggesting that the initial 29 species value in Table 1 may reflect an already decreasing level of diversity. Stands over 400 years of age were similarly difficult to locate with the result that it could not be determined if a nearly all-aged forest develops with continued high diversity, or if a new pulse of regeneration occurs with subsequent canopy closure and species loss. Probably both situations can occur depending on the nature of tree mortality in the later stages of succession with increasingly synchronous mortality leading to increasingly dense regrowth.

Developmental patterns similar to that shown in Table 1 occur in many *Picea*, *Abies* forests, some *Pinus flexilis* forests and in the denser *Pseudotsuga* forests. Table 2 shows a typical sequence for *Picea*, *Abies* forests which is strikingly similar to that shown for *Pinus contorta* forests in Table 1. The only major difference is that the depression

Table 2. A developmental sequence of middle elevation *Picea engelmannii*, *Abies lasiocarpa* stands illustrating changes in forest structure and species richness.

Age (years)	Seedlings (N/ha)	Saplings (N/ha)	Trees (N/ha)	Basal Area (m ² /ha)	Species (S/0.1 ha)
73	4740	1580	1200	13.4	28
~200	2290	890	1260	34.8	7
~350	2070	290	1070	66.0	21
>500	5090	860	640	41.2	23

of diversity and biomass increment in the middle portion of the sequence is not as pronounced.

Table 3 illustrates what happens on more extreme sites, either at very high elevations or on very dry sites at middle elevations. Sites such as those which support the *Picea*, *Abies* stands shown in Table 3 recover very slowly from disturbance. Canopy development rarely or never reaches the point of depressing tree regeneration. Similarly, the mid-sequence depression in diversity is not found. Rather, diversity increases to a peak early in forest development and then drops gradually as tree density and reproduction increases. (Note that the first two stands in the sequence are of the same age and actually originated after the same fire. The first is in an earlier stage of development, however, owing to more exposed site conditions.)

Comparisons with developmental patterns for other site conditions indicate that the results seen in Tables 1–3 can be generalized. For stands on favorable sites diversity varies dramatically, along with biomass and productivity as shown in Fig. 3a. In this idealized representation, post-disturbance stand development is characterized by initially rapid tree establishment. Formation of a closed tree canopy quickly follows with light being greatly reduced in the interior of the stand. The preemption of light and perhaps nutrient and water resources by canopy individuals results in temporary elimination of tree seedling establishment and most herbaceous growth. Similarly, tree growth is soon inhibited by crowding with the result that productivity drops and biomass levels off. Eventually, mortality of canopy trees through natural thinning allows sufficient light to penetrate the canopy for tree regeneration and

Table 3. A developmental sequence of high elevation *Picea engelmannii*, *Abies lasiocarpa* stands illustrating changes in forest structure and species richness.

Age (years)	Seedlings (N/ha)	Saplings (N/ha)	Trees (N/ha)	Basal Area (m ² /ha)	Species (S/0.1 ha)
75	180	60	50	0.9	57
75	4520	380	270	7.4	38
150	290	70	720	24.3	28
>450	1710	620	980	39.0	29

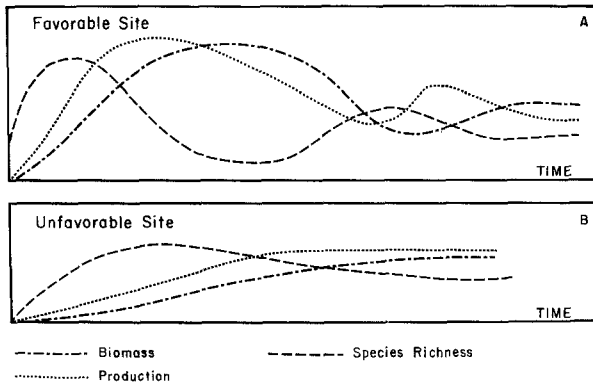


Fig. 3. Generalized developmental patterns for forests of the Colorado Front Range. The favorable site (A) is typical of *Pinus contorta*, *Pseudotsuga menziesii*, and *Picea engelmannii* dominated forests at middle elevations. Time scales will vary with forest type, with the secondary low in biomass occurring around 275 years for *Pinus contorta* and around 450 years for *Picea engelmannii*. The unfavorable site (B) is typical of higher elevation *Picea*, *Abies* forests and xeric or exposed sites dominated by *Pinus flexilis*.

herb diversity to increase. This form of stand development is similar to that in some Scandinavian boreal forest studies (e.g. Ilvessalo 1937, Siren 1955).

On xeric, or high-elevation, alpine-transition sites a different pattern of forest development as usually found (Fig. 3b). Here diversity either increases steadily with approach to climax, or else rises to a moderate but early peak and then decreases slightly with canopy development (as in Table 3). These are environmentally rigorous sites for plant growth and establishment with the result that the canopy does not develop as rapidly as on most of the more favorable sites. Rather, forest development is a slow process with the forest rarely or never attaining a density sufficient to preclude tree regeneration or herbaceous growth.

From these results, it appears that successional patterns of diversity change for Front Range forests must be expressed in the context of the environmental gradients which most strongly influence successional development. Moreover, the resultant patterns are as much a consequence of patterns in forest tree establishment and growth as they are of the intrinsic characteristics of the site.

Stratal Relationships

Species richness has frequently been observed to vary independently for different strata within a community

(Auclair & Goff 1971, Daubenmire & Daubenmire 1968, Glenn-Lewin 1975, 1977, Whittaker 1960, 1972, 1977, Zobel et al. 1976). This suggests that dissection of communities into stratal components or synusia might improve interpretability. For the present study species were classified as trees, shrubs, or herbs with richness (species per 0.1 ha) within each stratum being plotted on the gradient diagram (Fig. 4). In addition, correlations between species number and/or cover for the three strata were examined using Spearman rank correlation statistics (Table 4).

As herbs are the primary determinant of richness or species number, it is not surprising that their pattern is roughly parallel to that of total species richness. Tree species richness (Fig. 4a) was found to be highest in the wet-mesic, mid-elevation forests with a secondary maximum in high elevation, dry sites. Shrub richness (Fig. 4b) was similarly seen to peak in the wet-mesic, mid-elevation forests and generally decrease with elevation, but the moisture response appears less pronounced than for tree richness. This absence of a distinct moisture gradient for shrub richness perhaps results from the complementary effects of increasing available moisture and decreasing light penetration to the shrub stratum.

The dense coniferous forests of the central portion of the gradient representation have the lowest richness encountered, largely owing to their lack of understory herbs. Dense tree canopies are frequently suggested to reduce herb richness by light preemption (Auclair & Goff 1971, del Moral 1972, Whittaker 1965, 1960, 1972). Table 4 allows a partial examination of the relationship of canopy to diversity. Shrub species richness shows a strong negative correlation with tree cover, and a strong positive correlation with herb cover. Thus, shrub diversity appears directly related to those conditions under which herbaceous species have ample resources for growth. Herb species diversity is also strongly correlated with conditions appropriate for herb growth (herb cover) and the data also suggest a possible (though not statistically significant) negative correlation with increased light preemption (cover) by trees.

Geographic Relationships

One aspect of species diversity of considerable interest but which is especially difficult to document is geographic variation. While community diversity is known to vary along geographical gradients (see Cody 1975, Whittaker 1960, 1972), such gradients are hard to quantify and only

Table 4. Spearman rank correlations for percent cover and species number per 0.1 ha within tree, shrub and herb strata.

	Tree species	Shrub species	Herb species	Tree cover	Shrub cover	Herb cover
Tree species	1.0	0.2013*	-0.0409	0.3549**	0.1648*	-0.0647
Shrub species	0.2013*	1.0	0.3510**	-0.2431**	0.1045	0.2344**
Herb species	-0.0409	0.3510**	1.0	-0.1067	-0.0333	0.8003**
Tree cover	0.3549**	-0.2431**	-0.1067	1.0	0.3308**	-0.0128
Shrub cover	0.1684*	0.1045	-0.0333	0.3308**	1.0	0.0375
Herb cover	-0.0647	0.2344**	0.8003**	-0.9128	0.0375	1.0

* = significant at 0.01 level

** = significant at 0.001 level

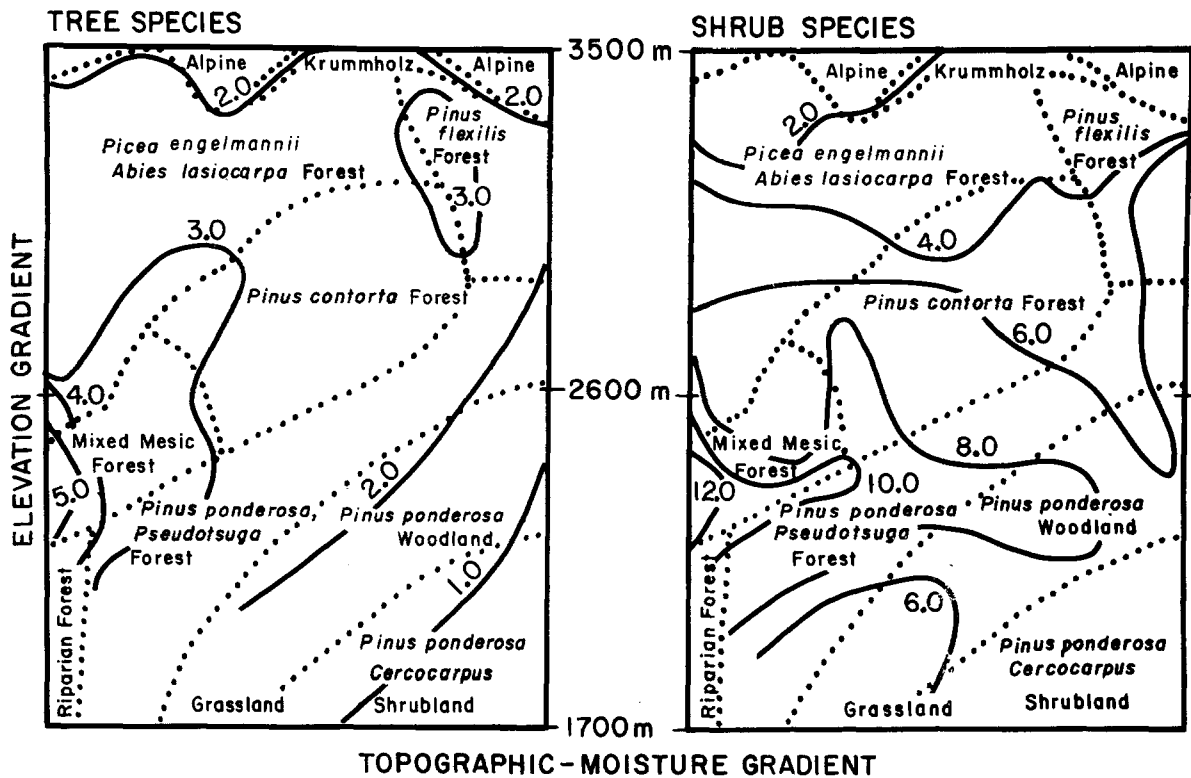


Fig. 4. Tree and shrub species richness per 0.1 ha relative gradients of elevation and topographic moisture. Herbaceous to species richness roughly parallels the pattern of total species richness shown in Fig. 1.

scattered data are available. Comparison with available studies containing richness values for neighboring areas (Bunin 1975, Despain 1973, Moir 1969, Oosting & Reed 1952, Pfister 1972, Reed 1969, Wirsing 1973) revealed the communities of the Front Range to be typical of the forests of the central Rocky Mountains, though perhaps somewhat richer. No geographical trends were evident.

Expanding comparisons to all North American vegetation revealed the peripheral communities on the gradient representation to have remarkably high richness for a floristically depauperate region (see Daubenmire 1943). Table 5 lists species counts from representative 0.1 ha samples throughout North America. Whittaker (1965, 1972) considered the Sonoran desert on the south-slope of the

Table 5. Selected species richness values for 0.1 ha plots.

Forest type	Location ¹	No. species
<i>Tsuga - Rhododendron</i> Forest	GSM	6
<i>Picea - Abies</i> Forest	GSM	19, 21, 22
<i>Pinus pungens</i> Forest	GSM	29, 42
Deciduous Cove Forest	GSM	61
Cove Forest Transition	GSM	68
Mixed Mesic Forest	HNC	85 - 95
Mesic <i>Pinus taeda</i> Forest	DF	95 - 115
<i>Pinus muricata</i> Forest (0.025 ha)	MC	12.4
<i>Sequoia sempervirens</i> Forest (slopes)	MC	23.4
Subalpine Forest	SCM	8.3
Montane <i>Abies</i> Forest	SCM	13.7 (+1) ²
<i>Pinus ponderosa-Quercus</i> Woodland	SCM	17.9 (+2)
Open <i>Quercus</i> Woodland	SCM	37.6 (+8)
Montane ravine	SCM	41.5 (+10)
Sonoran desert scrub	SCM	62.6 (+20)
Lower Bajada	SCM	9.3
<i>Tsuga canadensis</i> Forest	NY	19.4
<i>Fagus grandidentata</i> Forest	NY	29.0
Mixed mesophytic Forest	NY	45.0
<i>Abies</i> Forest	FLB	15.9
Mixed Forest	FLB	13.6
Moist Tropical Forest (trees only)	BCI	100.2

¹ Locations and References: GSM = Great Smoky Mountains, Whittaker 1965; HNC = Highlands, North Carolina, T.R. Wentworth, personal communication; DF = Duke Forest, North Carolina, Peet & Christensen, unpublished; MC = Mendicino County California, Westman & Whittaker 1975; SCM = Santa Catalina Mountains, Whittaker & Niering 1965; NY = Tompkins County, New York, Glenn-Lewin 1975; FLB = Findley Lake Basin, del Moral 1973. BCI = Barro Colorado Island, Knight 1975.

² (+N): N = correction added for rare herbs not in the 25 m² quadrats (personal communication, Whittaker 1975).

Santa Catalina Mountains and the cove forests of the Smoky Mountains with between 60 and 70 species per 0.1 ha to be, within his experience, among the richest communities in North America. His next richest community types had fewer than 47 species per 0.1 ha plot. T. R. Wentworth (personal communication) has found 85 to 95 species per 0.1 ha to be typical of the rich cove forests of mountainous North Carolina. Working in mesic, late successional *Pinus taeda* forests on the North Carolina piedmont, Peet & Christensen (unpublished) have found species richness to vary between 85 and 115 species per 0.1 ha. In the present study the sites with highest richness were the mid-elevation, wet-mesic forests which had an average of 60.3 species per plot (ranging up to 82) placing them among the most diverse of the types sampled by Whittaker. Twenty-five samples from the present study

representing mostly mid-elevation, wet-mesic forests and foothill woodlands had in excess of 47 species suggesting these types to be unusually rich in species for western North American vegetation.

Other sources of data from potentially diverse coniferous forests were sought in the literature. The presumably species rich coniferous forests of the Pacific Northwest (Daubenmire 1943) appear not to have communities averaging over 35 species per 0.1 ha (del Moral 1972, 1973, Douglas 1972, Zobel et al. 1976). The richest montane or boreal coniferous forests known to the author were reported from the Candle Lake, Saskatchewan forests where Jeglum (1972) found *Larix laricina* and *Picea mariana* swamps averaging 40 species per plot (each apparently 30 quadrats of 0.5 × 0.5 m), though Swan & Dix (1966) reported much lower richness values for upland sites in the same area.

Heterogeneity indices were also compared, these having the advantage of being sample size independent. The peripheral forest communities of the Front Range are the most diverse yet reported for temperate coniferous forests. Both the mixed mesophytic forests of the southern Appalachians ($N_1 = 8.00$, Monk 1967) and the most diverse communities of the Pacific Northwest ($N_1 = 9.9$, del Moral 1972) are lower than the wet-mesic mid-elevation forests (maximum $N_1 = 23.1$) and the *Pinus ponderosa* woodlands (typically $N_1 = 10-15$) of the Front Range.

That the supposedly species-poor forests of the Front Range should be included among the most diverse forests of North America is unlikely. The reports by Wentworth, and Peet & Christensen of markedly more diverse forests in North Carolina suggest that insufficient comparative data are available. It is likely that with further investigation, grassland-forest ecotones and mesic foothill ravine forests along the length of the Rocky Mountains will prove equally diverse as those of the Front Range. Probably the richness observed by Whittaker in the Santa Catalina Mountains is not as unusual as first appeared, but is characteristic of dryland ecotones, both grassland-forest and semidesert-grassland. If true, similar species-rich vegetation should be found throughout much of the interior of western North America.

Beta diversity

Wealth in species can be studied at several levels in addition to that of the sample plot. Whittaker (1960, 1965, 1972) suggested three distinct levels of diversity: plot diversity

(alpha-diversity), compositional change across a gradient (beta-diversity), and the total landscape diversity (gamma-diversity). Cody (1975) proposed four levels of diversity: point, plot, change across local environmental gradients, and change across macro-geographic gradients. Whittaker's beta is among the easiest to quantify of the higher levels of diversity because it can be measured either as rate of change or as gradient length. Beta diversity is conceptually significant in that it is directly related to species packing characteristics of community gradients. Environmentally favorable and predictable conditions should be expected to have high species packing and beta diversity, whereas strong fluctuations or high stress levels should keep beta diversity levels low (Leigh 1975, MacArthur 1969, 1970 MacArthur & Levins 1967, May 1973, Whittaker 1972).

Table 6 lists beta diversity values as gradient lengths for an elevational sequence of six moisture gradients, and a sequence of five elevational gradients for corresponding moisture conditions. Along both series of gradients, beta-diversity is lowest in the central portion where apparently strong competition from coniferous trees precludes rich understory development. Moisture gradients at low elevations have higher beta values than those at high elevations. This can be attributed to several factors. 1) The range of available environmental conditions at low elevations is greater than at high elevations. 2) The lower elevation environment is not as severe. 3) High-elevation forests are geographically isolated from source areas and thus have a smaller pool of available species. In this regard, the high-elevation vegetation might presently be losing species in response to a decrease in area following the last glacial retreat; undergoing relaxation in the terminology of Diamond (1972). A similar pattern has been reported for high-elevation mammals (Brown 1971). In contrast, the Front Range is adjacent to a vast source area of semi-arid vegetation to the south and east, but disjunct from larger areas of cool or mesic vegetation.

Table 6. Beta diversity values for moisture and elevation gradients. Units are in half-changes and refer to gradient length.

1) Six moisture gradients from low elevation to high:	4.91	2.81	3.34	1.45	3.30	2.97
2) Five elevation gradients from mesic to xeric:	4.16	2.09	2.05	2.77	7.16	

Conclusions

To understand diversity patterns a necessary first step is to place these patterns in appropriate perspective. Diversity values are exceptionally difficult to interpret when taken out of context, and little justification exists for their publication if such perspective is not provided. The data presented above suggest that environmental, successional and geographical patterns should be considered in diversity interpretation.

Environmental perspective

One likely reason for the failure of general diversity patterns to emerge from the many published case studies has been the reluctance of investigators to formulate multidimensional models. Contradictory, unidimensional trends in diversity with elevation or site moisture status can be obtained from a single data set when interactions are not considered, whereas simultaneous examination of these two factors can often remove the ambiguity. For this reason variation relative to all major environmental gradients should be examined simultaneously. Only in this way can diversity patterns involving interactions of contributing factors be resolved.

One of the few published attempts at multidimensional representation and analysis of diversity patterns is that of Auclair & Goff (1971) who represent diversity changes through time as a function of environmental rigor. These workers suggest that after perturbation, mesic sites show an initial rise to high diversity followed by a pronounced drop with canopy development and the onset of climax conditions. In contrast, on the extreme sites, diversity is suggested to increase steadily toward a steady-state maximum. The model was designed for the mesic, mixed-deciduous forests of the Lake States where stand stagnation and canopy breakup such as occurs in Rocky Mountain forests is uncommon. To generalize this model to conform to the patterns observed for Rocky Mountain forests requires extension of the time gradient to include an eventual increase in diversity during the approach to all-aged conditions on mesic sites (Fig. 5). That the Rocky Mountain model and the Auclair and Goff model can be combined to represent much of the variation in diversity found in both regions underlines the importance of multidimensional approaches to diversity studies.

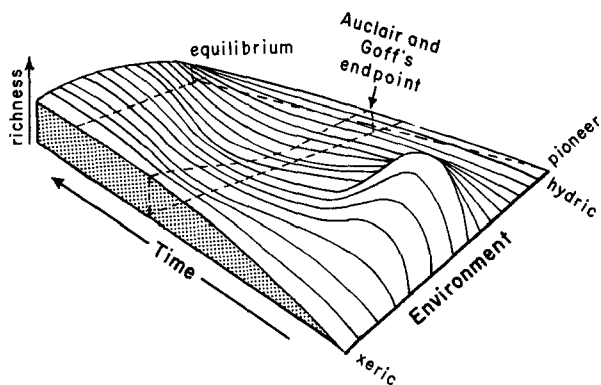


Fig. 5. A generalization of the Auclair-Goff model of forest diversity to accommodate forests of the Colorado Front Range.

Historical perspective

Examination of environmental factors impinging directly on plants ('operational environment' of Mason & Langenheim 1957), while important for interpretation of local patterns, has not proven sufficient for explanation of variations in diversity between localities. Diversity reflects species evolutionary history as well as site history. While speciation, competition, immigration, adaptation and extinction are all important processes, it is virtually impossible to separate their relative influence in determining community structure.

Rocky Mountain forests illustrate this difficulty. These are disturbance forests; the component species evolved primarily in the context of periodic perturbation rather than climax conditions (see Loucks 1970, Taylor 1973). Recurring environmental perturbations such as fire have been suggested to reduce the number of species which can be maintained in a community (May & MacArthur 1972, Sanders 1969, Slobodkin & Sanders 1969). However, evolution in the presence of fluctuation and disturbance can lead to an increase in the number of species maintained (Loucks 1970, Abele 1976). Or, simply the presence of a mosaic of disturbance-maintained patches can allow an increase in the number of coexisting species (Levin 1974). The net affect on regional diversity is hard to predict, but diversity of Front Range forests clearly must be considered in the context of evolutionary response to a spatial-temporal disturbance mosaic. It is likely that a change in the disturbance regime of these forests, whether natural or man-induced, would have an initial consequence of reducing species diversity.

Diversity responses to environmental conditions will

vary as a result of evolutionary and environmental history. The failure of generalized diversity models such as proposed by Terborgh (1973), Monk (1967), and Connell & Orias (1964) or as sought by Glenn-Lewin (1977) and Whittaker (1977) similarly reflects the difficulty of generalizing the impact of historical factors.

Alternative approaches

Failure of broad, geographic patterns of plant species diversity to readily emerge from this and other studies suggests that alternative approaches are needed. One approach is to change the scale of investigation. Perhaps diversity should be examined at the scale of the entire community rather than just vascular plants. Many important species interactions are not considered if the entire community is not studied (Menge & Sutherland 1976).

Alternatively, vascular plants can be considered to form a much too complex group to analyze as a whole, just as do all animals together. Advances made in understanding animal community structure have come from studies of restricted taxocenes such as birds or lizards. In the present study, simply dividing the vegetation into three vertical strata aided greatly in interpretation. If plant diversity is to be understood, we will probably need to concentrate more on investigations of relatively small groups of directly competing individuals. The guild concept of Root (1967) might provide a workable approach, or the descriptive, growth and life form classifications of such early ecologists as Rubel or Raunkiaer might profitably be revived.

Summary

Plant species diversity patterns of the Rocky Mountain forests were found to be at variance with patterns reported from other regions. The most centrally located forests in terms of elevation, site moisture and successional status were found to have the lowest diversity. In contrast, the peripheral and environmentally more severe sites were found to have relatively high diversity. In particular, the forest-grassland transition and the low elevation riparian forests have species diversity values as high as any yet reported from western North America.

When diversity was examined in terms of variation across elevation or moisture gradients, varying results were

obtained due to the interaction of these factors. The failure of previous studies to converge on generalizations about plant diversity reflects, in part, the failure of most investigators to view diversity in a regional context of variation across several interacting gradients.

Diversity was seen to vary inversely with the degree of development of the forest canopy. The interaction of different components of the forest community is one reason for the failure of general patterns of plant species diversity to emerge from previous studies. A potentially rich herb community can be greatly suppressed by a single species tree stratum.

Among the most successful work to date on species diversity is that on birds, a distinct albeit large and functional group. It is unlikely that similar success could have been achieved through work on all animal species simultaneously. This suggests the need to examine plant species diversity, not in terms of total diversity, but in terms of component functional groups, perhaps guilds, growing under similar microclimatic conditions and subject to similar competitive pressures.

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